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Nematodes Associated with Bark Beetles, with Focus on the Genus *Ips* (Coleoptera: Scolytinae) in Central Europe

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Abstract: The relationships between nematodes and *Ips* spp. has been a neglected topic in central Europe. This work summarizes available informations on entomophilic nematodes associated with bark beetles (Scolytinae) with focus on the genus *Ips* De Geer, 1775. The association can be phoretic, in which the nematode uses the bark beetle for transport to a new environment. This is the case of *Bursaphelenchus*, *Cryptaphelenchus*, *Ektaphelenchus*, *Fuchsnema*, *Micoletzkya*, *Neoditylenchus* and *Plectus* species, while the most frequent phoretic nematodes in *Ips* bark beetles are *Bursaphelenchus eidmanni* (Ruhm, 1956) and *Micoletzkya buetschlii* (Fuchs, 1915) or endoparasitic, in which the nematode enters and obtains nutrients from the host beetle and depends on the beetle for completion of its life cycle, the case of *Contortylenchus*, *Cryptaphelenchus*, *Ektaphelenchus*, *Parasitaphelenchus*, *Parasitorhabditis* and *Parasitylenchus* species. The most frequent endopararasitic nematode in *Ips* species are *Parasitylenchus dispar* (Fuchs, 1915) and *Contortylenchus diplogaster* v. Linstow, 1890. The effects of nematodes on beetle hosts are discussed. Lists of the nematodes associated with particular *Ips* species in central Europe are provided, also the little that is known about these associations in central Europe is summarized.

Key words: Scolytinae, nematodes, phoresy, endoparasitism

Introduction

Nematodes (Phylum Nematoda) are among the most numerous and abundant animals. More than 24,000 species are currently known (Hugot *et al.* 2001), although as many as 1 million species are thought to exist. Therefore, this phylum could be comparable in size to the class Insecta, which is represented by approximately 925,000 described species (Grimaldi, Engel 2005).

Nematodes live in all types of environments. A large numbers of free-living, terrestrial, freshwater and of course saltwater species of nematodes are known. They display various life strategies and enter into numerous interactions with viruses, bacteria, plants, fungi, and other animals. Many nematodes are parasites of plants, invertebrates, and vertebrates, including humans. Representatives of this phylum are also frequently used as model organisms in research.

Nematology developed rapidly in the second half of the 20th century and became a well-developed discipline with a number of sub-disciplines, its own techniques, and a substantial literature. Nematode systematics benefitted from the introduction of the electron microscope in the 1960s, of PCR in the 1980s (Ferris 1994), and of other molecular techniques more recently. Today, the classification and phylogenetic relationships within the Nematoda is the focus of substantial part of research, and many new species continue to be described.

The aim of this article is to summarize the current knowledge of the nematodes associated with bark beetles (i.e., beetles in the subfamily Scolytinae), with particular focus on the bark beetles of the genus *Ips* De Geer, 1775 in central Europe. The present knowledge concerning nematodes of bark beetles is very fragmentary, and the topic has largely been ignored in central Europe.

Entomophilic nematodes

Publications concerning entomophilic nematodes (i.e., nematodes closely associated with insects) range from those that merely delineate an association to more detailed studies that describe the relationship between nematode and insect. These relationships include saprobiotism (living in decaying material), commensalism (benefit without affecting the other), which is, according to KAYA, STOCK (1997), one of the most common relationships between nematodes and insects, phoresy, and various degrees and types of parasitism (such as semi-parasitism commonly parasitic but also capable of living on dead or decaying animal matter, ectoparasitism- living on the body surface of the host, endoparasitism- living within the host, facultative parasitism- living independent of at he host but may occasionally be parasitic under certain conditions, and obligate parasitism- cannot complete its life cycle without exploiting a suitable host (e.g., WEISER 1988, TENKACOVA, MITUCH, 1987, 1991).

Phoretic nematodes occur on the body and limbs, in the inter-segment spaces, and under the wings of beetles, flies, and other insects. These nematodes instinctively leave a drying substrate and attach themselves to an insect, which transports them to a new environment. In the new environment, the phoretic nematodes leave the insect and feed on fungi, bacteria, and other microorganisms (NICKLE, 1973). Nematodes are also found in the reproductive, respiratory, gastrointestinal, and excretory systems of insects. These endoparasitic nematodes can damage or kill their hosts. Entomophilic, especially entomopathogenic nematodes (nematodes that live within and that weaken and sometimes kill their host insects) have been studied by WEISER (1966), NICKLE (1973), POINAR (1975), WEISER, MRACEK (1988), SONIN, SHARMA (1990) SIDDIQI (2000), GAUGLER (2002), NGUYEN, HUNT (2007), and many others.

For more than 50 years, many researchers have studied entomopathogenic nematodes as biological control agents of insect pests. Much of this research has been focused on nematodes of the families Heterorhabditidae and Steinernematidae, which have wide host ranges (NERMUT *et al*. 2012). Biological control of insect pests by entomopathogenic nematodes has been studied by GAUGLER, KAYA (1990), SCHEEPMAKER *et al*. (1997), STURHAN, LISKOVA (1999), FENTON *et al*. (2000), NAVON, ASCHER (2000), WILSON, GAUGLER (2004), GEBREMARIAM *et al*. (2005), and many others.

Entomophilic nematodes of bark beetles

Entomophilic nematodes were first studied in the 19th century, and one of the first works dealing with relationships between nematodes and bark beetles was written by VON LINSTOW (1890), wherein he described the nematode *Allantonema diplogaster* (later renamed *Contortylenchus diplogaster* by RUHM (1956)) in the spruce bark beetle *Ips typographus* (LINNAEUS, 1758) (MASSEY 1974). Since that time, in many publications species of nematodes found in various bark beetles have been described (e.g., FUCHS 1914, 1915, 1929, 1930, OLDHAM 1930, STEINER 1932, THORNE 1935, 1949). Important work in this period included FUCHS (1915), which described nematodes associated with *I. typographus*, and FUCHS (1938), which is a taxonomic study of nematodes in the superfamilies Aphelenchoidea and Tylenchoidea. The interest in entomophilic nematodes has increased since the 1950s (ANDRASSY 1954, WACHEK 1955, MASSEY 1957, 1960, 1964ab, 1969, NICKLE 1967, 1970, THONG,WEBSTER 1973, HUNT, HAGUE 1974, GERAERT, DE GRISE 1981, TOMALAK *et al*. 1989, KAYA, STOCK 1997, BRAASCH 2001, RYSS *et al*. 2005). These publications include a number of taxonomic keys focusing on individual nematode families and genera. There are also publications dealing with nematodes associated with individual species of the following genera of bark beetles: *Scolytus* (MASSEY 1964a, ASHRAF 1968, ASHRAF, BERRYMAN 1970, HUNT, HAGUE 1974, MOSER *et al*. 2005), *Dendroctonus* (MASSEY 1956, 1966, FURNISS 1967, THONG, WEBSTER 1983), *Pityogenes* (REID 1958, NICKLE 1963), and *Ips* (RUHM1954, 1955, 1956, MASSEY 1960, HOFFARD, COSTER 1976). An important study by RUHM (1956) provided an overview of entomophilic nematodes associated with bark beetles from Germany and information about nematode life cycles. This study, which is still frequently cited, contains detailed characteristics of nematodes found in 14 genera of bark beetles (*Cryphalus, Crypturgus, Dendroctonus, Dryocoetes, Hylastes, Hylesinus, Hylurgus, Ips, Myelophilus, Orthotomicus, Pityogenes, Pityophthorus, Polygraphus* and *Scolytus*) and details on *Ips acuminatus* (GYLLENHAL, 1827), *I. amitinus* (EICHHOFF, 1871), *I. cembrae* (HEER, 1836) and *I. typographus*. Similar publications from the United States (MASSEY 1974, CHOO *et al*. 1987) described the entomophilic nematodes found in bark beetles including *Ips* species.

The nematodes associated with bark beetles are frequently studied along with other pathogens that could serve as biological control agents of beetle pests. However, the information on these nematodes is incomplete and often limited to easily discernible, endoparasitic species (i.e., nematodes within the beetle rather than on the beetle), such as *Contortylenchus* and *Parasitylenchus* spp. (e.g., WEISER *et al*. 2006, TAKOV *et al*. 2006, 2011, Burjanadze, Goginashvili 2009, Kereselidze *et al.* 2010, Michalkova *et al.* 2012).

Relationships between nematodes and bark beetles

Relationships between nematodes and bark beetles are described by the same terms as is the case for relationships between certain other organisms.

Phoretic nematodes

Phoresy is widespread between nematodes and bark beetles, and phoretic nematodes are commonly found on the bodies of beetles. They are most frequently located in clusters under the elytra, on the wings, or between the individual segments of the body, especially between the thorax and the abdomen and between abdominal tergites. These nematodes mostly consume fungi, bacteria, and other microorganisms, and they are often found on the bodies of beetles undergoing anabiosis. Groups of phoretic nematodes sometimes assume specific formations. Species in the genus *Ektaphelenchus*, for example, form cocoon-like structures (nematangia) under the elytra and on the wings of the beetle (Cardoza *et al*. 2006). The life cycle of these phoretic nematodes has a number of essential features. Adult nematodes occur in the beetle galleries, where they mate and generally lay eggs (oviparity) from which the second stage juveniles hatch. The juveniles moult several times and then seek their host. Upon attaching to the host beetle, they are transferred to a new environment, where they leave the host and continue to develop and moult. Upon reaching maturity, the adults mate, and the entire cycle is repeated. Examples of phoretic nematodes of bark beetles include species of *Neoditylenchus*, *Ektaphelenchus*, *Micoletzkya*, and *Bursaphelenchus*. Nematodes found on the bodies of *Ips* species in central Europe are presented in Table 1.

Parasitic nematodes

In contrast to phoretic nematodes, parasitic nematodes occur in the body cavities of their hosts and require hosts to complete their life cycle (Hunt, Hague 1974). In the case of parasites of bark beetles, endoparasitic nematodes are most frequently found moving freely in the body cavities of adults, larvae, and pupae. *Cryptaphelenchus* spp. are also found on the surface of the insect and in the Malpighian tubules, and *Parasitaphelenchus* and *Parasitorhabditis* spp. occur in the lumen of the intestine but also move freely in the body cavity. With respect to the life cycle of endoparasitic nematodes, juvenile nematodes mature and mate in bark beetle galleries. The impregnated pre-mature female infects the beetle, which is usually the 1st or 2nd stage larva, by passing through its cuticle or intestine. The life cycles of the parasite and host are synchronized, and the female nematode reaches maturity at approximately the same time as its host. The female then produces juveniles (e. g., *Parasitylenchus*) or eggs (e. g., *Contortylenchus*) within the host body cavity. Young nematode juveniles then penetrate the intestine and are emited into the gallery. A variation on this kind of life cycle is displayed by *Parasitaphelenchus* spp., which lay their eggs near host larvae in the gallery (e. g. Scolytus, *Ips*, *Polygraphus*, *Scolytus* genera). The nematode juveniles then hatch, and after several moults, infect the larvae or even the pupae of the bark beetle. They suck fluids within the beetle's body cavity, subsequently infect the intestine, and then leave the body and return to the gallery, where they moult into the adult stage, copulate, and lay eggs. The number of nematode generations per year is identical to the number of host generations per year, and can be as high 12 in laboratory experiments of *Contortylenchus elongatus* (Massey, 1960) Nickle, 1963 in *Ips confusus* (Le Conte, 1876) (Massey 1974). Endoparasitic nematodes associated with *Ips* bark beetles in central Europe are presented in Table 2.

The effect of parasitic nematodes on their hosts

Since the first studies of entomophilic nematodes of bark beetles, researchers have been interested in the effects of endoparasitic nematodes on the populations of these forest pests. Endoparasitic nematodes obtain nutrients from the host body fluids, and in some cases consume all of the host's fat body and other tissues. Endoparasitic nematodes are commonly found in bark beetles, and sometimes at infestation rates exceeding 50 % (e. g. Burjanadze, Goginashvili 2009). Massey (1974) considered nematodes to be important factors limiting the populations of bark beetles. Although these nematodes seldom kill their host, they can change host behaviour; decrease host fertility, survival, and flight activity, and delay swarming (e.g., Hoffard, Coster 1976, Kaya 1984). Fuchs, in his studies from the first half of the 20th century, stated that nematodes weaken and kill bark beetles, reduce the number of eggs laid by as much as 40 %, and reduce the number of generations per year (Massey 1974). Yatsenkowsky (1924) reported that infestation of bark beetles by small numbers of nematodes causes beetle sterility while infestation by large numbers causes death. Subsequent research has greatly increased our understanding of how endoparasitic nematodes affect insect hosts.

Nematodes developing inside the beetle deprive the host of nutrients. This is evidenced by a decreased number of fat cells in infected bark bee-

Table 1. Nematodes found under elytra, on the wings, thorax, abdomen and between body segments of *Ips* bark beetles in central Europe. For species marked with an asterisk (*) in the table see a list of known synonyms provided in Table 4

Nematode species	Nematode family	*Ips* species	Country	Reference
Bursaphelenchus eidmanni (Ruhm, 1956) *	Parasitaphelenchidae	*I. amitinus* *I. typographus*	Germany, Slovakia	Ruhm 1956, Tenkacova, Mituch 1986, 1987, 1991
Bursaphelenchus sexdentati Ruhm, 1960 *	Parasitaphelenchidae	*I. sexdentatus*	Germany	Ruhm 1960
Cryptaphelenchus macrogaster acuminati Ruhm, 1956	Aphelenchoididae	*I. acuminatus*	Germany	Ruhm 1956
Cryptaphelenchus macrogaster macrogaster (Fuchs, 1937) *	Aphelenchoididae	*I. cembrae* *I. typographus*	Germany, Slovakia	Ruhm 1956, Tenkacova, Mituch 1986, 1991
Ektaphelenchus amitini (Fuchs, 1937) *	Ektaphelenchidae	*I. amitinus*	Germany	Ruhm 1956
Ektaphelenchus typographi (Fuchs, 1930) *	Ektaphelenchidae	*I. typographus*	Germany	Ruhm 1956
Fuchsnema halleri (Fuchs, 1915) *	Diplogasteroididae	*I. amitinus* *I. cembrae* *I. typographus*	Germany, Slovakia	Ruhm 1956, Tenkacova, Mituch 1986, 1991
Micoletzkya buetschli acuminati (Micoletzky, 1922) *	Neodiplogastridae	*I. acuminatus*	Germany	Ruhm, 1956
Micoletzkya buetschlii (Fuchs, 1915)	Neodiplogastridae	*I. cembrae* *I. typographus*	Czech Republic, Germany, Slovakia	Weiser 1954, Ruhm 1956, Tenkacova, Mituch 1986, 1991
Neoditylenchus major (Fuchs, 1915) *	Neotylenchidae syn. Sychnotylenchidae	*I. amitinus* *I. typographus*	Germany, Slovakia	Ruhm 1956, Tenkacova, Mituch 1987, 1991
Plectus rhizophilus de Man, 1880	Plectidae	*I. sexdentatus*	Slovakia	Vilagiova 1990

tles, as described by Nickle (1963), Thong, Webster (1973), and Lieutier (1982). Depletion of nutrients (especially proteins) was confirmed by changes in the composition of the hemolymph caused by the development of a fertilized female of two *Contortylenchus* species in bark beetle hemocoel (Thong, Webster 1972, 1975). During beetle diapause, nematodes may also undergo dormancy, as described for the nematode *Paraiotonchium autumnale* (Nickle, 1967) Slobodyanyuk, 1976 (syn. *Heterotylenchus autumnalis* Nickle, 1967, which parasitizes certain flies. Otherwise, nematodes may infest the fat body, as is the case when *Mermis nigrescens* Dujardin, 1842 parasitizes grasshoppers (Thong, Webster 1975). Slankis (1967) also reported that nematodes caused mechanical damage to organs and tissues as well as intoxication. Great damage to the intestinal epithelium was found in *Ips sexdentatus* (Borner, 1776) parasitized by *Parasitorhabditis ipsophila* Lieutier and Laumond, 1978 (Lieutier 1984a).

The fact that endoparasitic nematodes significantly reduce bark beetle fertility was reported by Reid (1958), Massey (1956, 1960), Thong, Webster (1975), and Weiser, Mracek (1988). Smaller gonads in parasitized individuals had been previously described by Oldham (1930) (in Hunt, Hague 1974). Thong, Webster (1975) described a 20% reduction in oocytes. These structural changes might be direct effects or might reflect a general decrease in host nutrition caused by removal of nutrients by nematodes. This was confirmed by Lieutier (1982), who reported that individuals of *I. sexdentatus* parasitized by *Parasitaphelenchus* sp. and *Contortylenchus* sp. had smaller fat bodies and ovaries and less developed terminal oocytes than non-parasitized individuals. A small fat body is unable to provide the nutrients necessary for the normal maturation of oocytes, which therefore delays swarming and the start of oviposition. A slight decrease in the density of oviposition incisions and in the number of eggs in individuals parasitized by *Parasitorhabditis* sp. has also been reported (Lieutier 1984b). A shift in the time of swarming was confirmed by Nickle (1963) in *I. confusus*.

Nematode infection was reported to cause pathological changes in flight muscle structure of *Scolytus ventralis* LeConte, 1868 (Aschraf *et al.* 1971) but these changes may have been caused by a natural degradation (Forsse 1987). Subsequent research has not confirmed that nematode parasitism affects bark beetle flight capability. For example, nematode parasitism did not affect the flight activity of *Dendroctonus pseudotsugae* Hopkins, 1905 (Atkins 1961), *D. frontalis* Zimmermann, 1868 (Kinn, Stephen 1981), or *I. typographus* (Thalenhorst 1958, Forsse 1987).

Nickle (1971) as well as Poinar, Caylor (1974) stated that some nematode species can change insect behaviour and change the shape of bark beetle galleries. The shape of the galleries created by *I. sexdentatus*, however, was not changed by *Parasitorhabditis ipsophila* (Lieutier 1984b) or by *D. pseudotsugae* or *Contortylenchus reversus* (Thorne, 1935) Ruhm, 1956 (Thong, Webster 1975). Although nematodes did not change gallery shape, they did reduce gallery length by 25–28 % (Thong, Webster 1975)

The percentage of nematode-parasitized bark beetles in a population and the number of nematodes per beetle varies widely by location and probably depends on microclimate rather than on elevation or on whether the samples are collected from a standing or fallen tree. The reported prevalence of nematodes in bark beetles ranges from approximately 1 to 91 % (Takov, Pilarska 2008) but is frequently about 50–60 %. More than 99 % of galleries contained nematodes in the studies of Hoffard, Coster (1976), Tenkacova, Mituch (1986, 1987, 1991), Cardoza *et al*. (2008), Burjanadze, Goginashvili (2009), and Kereselidze *et al*. (2010). Significant differences have been documented in the parasitization rates between the spring and summer generations of beetles (Choo, Kaya 1987, Tenkacova, Mituch 1986) but not between male and female beetles (e.g., Zitterer 2002, Takov, Pilarska 2008).

A single bark beetle may contain many nematodes, and it is not unusual to find a bark beetle with hundreds of nematode juveniles in its intestine and hemocoel and under its elytra (Nickle 1973). Thong, Webster (1975) and Weiser (1966) found more than 1,000 eggs and juveniles of *Contortylenchus* spp. in the hemocoel of individual *Dendroctonus* and *Ips* beetles. The large number of nematodes per beetle results from the high fecundity of entomopathogenic nematodes; one female can produce as many as 10,000 juveniles (Nickle 1973).

Although each species of bark beetle is usually attacked by only a subset of the species of entomopathogenic nematodes (Cardoza *et al*. 2006), the number of nematode species associated with a single species of bark beetle can be variable. Ruhm (1956) recorded a maximum of 11 species of nematodes in the black pine bark beetle *Hylastes ater* (Paykull, 1800) in Germany, and Massey (1974) found 30 species in *Dendroctonus adjunctus* Blandford, 1897 in the United States.

Nematodes associated with *Ips* spp.

Bark beetles of the genus *Ips* belong to the family of snout beetles (Curculionidae) and the Scolytinae subfamily. In central Europe, seven species occur (*Ips acuminatus, I. amitinus, I. cembrae, I. duplicatus* (Sahlberg, 1836)*, I. mannsfeldi* (Wachtl, 1879)*, I. sexdentatus,* and *I. typographus*). An identification key to the bark beetle species, including *Ips* spp., was published by Pfeffer (1989). *Ips* spp. feed on the phloem of conifers, predominantly spruce, pine, and larch. These bark beetles have been often serious pests mainly in spruce monocultures but also in close-to-nature forests. Since 1950, 2–9 million m^3 of wood have been damaged annually by bark beetles, and predominantly by *I. typographus* (Schelhaas *et al.* 2003).

There have been very few studies of the nematodes associated with *Ips* spp. in central Europe. The first publication that described nematodes of *Ips* spp. in this region was by Weiser (1954), who described three species of nematodes found in the body and under the elytra of *I. typographus* (in Tenkacova, Mituch 1987). There are also several studies by Tenkacova, Mituch (1986, 1987, 1991) related to nematodes of *Ips* spp. in the territory of the former Czechoslovakia. The study sites in all of these reports were in the territory of today's Slovak Republic. Researchers have also reported on nematodes associated with *Ips* spp. in Germany (Ruhm 1956, 1960), Poland (Balazy 1966, 1968), Bulgaria (Takov *et al*. 2006; Nedelchev *et al.* 2008), Portugal (Penas *et al*. 2006), Russia (Slankis 1969), France (Lieutier, Laumond 1978), Sweden (Forsse 1987) and Georgia (Burjanandze, Goginashvili 2009).

Ips spp. have been reported to be associated with nematodes in the orders Diplogasterida, Rhabditida, and Tylenchida and in the families Parasitaphelenchidae, Allantonematidae, Ektaphelenchidae, Aphelenchoididae, Diplogasteroididae, Neodiplogasteridae, Rhabditidae, and Parasitylenchidae. Ruhm (1956) recorded nine species of nematodes in *I. typographus*, including five each in *I. acuminatus* and *I. cembrae* and three in *I. amitinus*. Massey (1974) found 4-14 species of nematodes in *Ips* spp. in the United States. The nematodes associated with *Ips* spp. range in size from 0.2 mm (*Cryptaphelenchus*) to 2.0 mm (*Contortylenchus*).

Lists of nematodes associated with *Ips* spp. in central Europe is given in Tables 1-3. A problem in preparing this kind of list is the existence of many

Table 2. Endoparasitic nematodes associated with *Ips* species in central Europe. For species marked with an asterisk (*) in the table see a list of known synonyms provided in Table 4

Nematode species	Nematode family	*Ips* species	Location	Country	Reference
Contortylenchus acuminati Ruhm, 1956	Allantonematidae	*I. acuminatus*	hemocel	Germany	Ruhm 1956
Contortylenchus amitini Ruhm, 1956	Allantonematidae	*I. amitinus*	intestinum	Czech Republic, Germany, Slovakia	Ruhm 1956, Weiser *et al.* 2006, Vilagiova 1993
Contortylenchus diplogaster v. Linstow, 1890 *	Allantonematidae	*I. cembrae* *I. sexdentatus* *I. typographus*	hemocel	Czech Republic, Germany, Poland, Slovakia	Ruhm 1956, Tenkacova, Mituch 1986, 1991, Balazy 1966, 1968
Cryptaphelenchus macrogaster acuminati Ruhm, 1956	Aphelenchoididae	*I. acuminatus*	Malphigian tubules intestinum	Germany	Ruhm, 1956
Cryptaphelenchus macrogaster macrogaster (Fuchs, 1937) *	Aphelenchoididae	*I, cembrae* *I. typographus*	Malphigian tubules intestinum	Germany, Slovakia	Ruhm 1956, Tenkacova, Mituch 1986, 1991
Ektaphelenchus typographi (Fuchs, 1930) *	Ektaphelenchidae	*I. typographus*	larvae	Germany	Ruhm 1956
Parasitaphelenchus acuminati Ruhm, 1956	Parasitaphelenchidae	*I. acuminatus*	hemocel intestinum	Germany	Ruhm 1956
Parasitaphelenchus sexdentati Fuchs, 1937 *	Parasitaphelenchidae	*I. sexdentatus*	hemocel intestinum	Czech Republic, Germany	Weiser, Mracek 1988, Filipjev 1959
Parasitorhabditis acuminati (Fuchs, 1937) *	Rhabditidae	*I. acuminatus*	hemocel intestinum	Germany	Ruhm 1956
Parasitorhabditis amitini (Fuchs, 1915) *	Rhabditidae	*I. amitinus*	intestinum	Germany, Slovakia	Ruhm 1956, Tenkacova, Mituch 1987, 1991
Parasitorhabditis obtusa (Fuchs, 1915) *	Rhabditidae	*I. cembrae* *I. typographus*	intestinum	Austria, Switzerland, Czech Republic, Germany, Poland, Slovakia, Slovenia	Ruhm 1956, Weiser, Mracek 1988, Tenkacova, Mituch 1986, 1987, 1991, Balazy 1966, 1968, Andrassy 1983
Parasitylenchus dispar (Fuchs, 1915)*	Parasitylenchidae	*I. typographus*	hemocel	Czech Republic, Germany, Poland, Slovakia, Slovenia	Ruhm 1956, Balazy 1966, 1968, Weiser 1954, 1977, Weiser, Mracek 1988, 2006, Tenkacova, Mituch 1986, 1991

synonyms for nematode species. Not all of them are valid (see Table 4). Synonyms of the Genus *Bursaphelenchus* were published by Ryss *et al.* (2005), *Contortylenchus*, *Neoditylenchus* and *Parasitylenchus* by Siddiqi (2000), *Micoletzkya* and *Fuchsnema* by Sudhaus, von Lieven (2003), *Parasitaphelenchus* by Ruhm, 1956 and the others by Baker (1962).

Conclusion

As between other organisms various relationships from commensalism to obligate parasitism occur between bark beetles and nematodes. Nematodes are almost always found in the galleries of bark beetles and each nematode species may benefit from the proximity of the bark beetle differently. Endoparasitic nematodes even can affect some important biological processes such as host fertility, survival, flight activity or swarming time, or change host behaviour . This review summarizes mentioned relationships and lists the known nematodes associated with the representatives of *Ips* genus which are importaint pests in Central Europe. Nematodes associated with *Ips* species could live as commensals using only bark beetle gallery environment (such e. g. members of *Clarkus*, *Panagrolaimus* or *Pristionchus* genera), phoretic nematodes use bark beetles for transfer to a new environment (e. g. memebers of *Bursaphelenchus* or *Micoletzkya* genera), to inhabit bark beetle body cavity is essential for endoparasitic nematode life cycles (e. g. *Contortylenchus* and *Parasitylenchus* genera) but some nematodes are

Table 3. Nematodes found only in frass and feed marks of *Ips* bark beetles in central Europe

Nematode species	Nematode family	*Ips* species	Country	Reference
Clarkus papillatus (Bastian, 1865)	Mononchidae	*I. typographus*	Slovakia	Vilagiova, 1990
Cuticularia oxycerca (de Man, 1895)	Rhabditidae	*I. sexdentatus*	Slovakia	Vilagiova, 1990
Mesorhabditis oschei Körner, 1954	Mesorhabditidae	*I. sexdentatus*	Slovakia	Vilagiova, 1990
Panagrolaimus chalcographi Fuchs, 1930	Panagrolaimidae	*I. typographus*	Slovakia	Vilagiova, 1990, 1993
Panagrolaimus rigidus (Schneider, 1866)	Panagrolaimidae	*I. sexdentatus*	Slovakia	Vilagiova, 1993
Prionchulus muscorum (Dujardin, 1845)	Mononchidae	*I. typographus*	Slovakia	Vilagiova, 1990
Pristionchus lheritieri (Maupas, 1919)	Neodiplogastridae	*I. typographus*	Slovakia	Vilagiova, 1990
Tripyla filicaudata de Man, 1880	Tripylidae	*I. sexdentatus*	Slovakia	Vilagiova, 1990

Table 4. Synonymous names of nematode species associated with Ips bark beetles in central Europe

Nematode species	Synonymous names
Bursaphelenchus eidmanni Rühm, 1956	*Aphelenchoides (Bursaphelenchus) eidmanni* Ruhm, 1956
Bursaphelenchus sexdentati Ruhm, 1960	*Aphelenchoides (Bursaphelenchus) sexdentati* Ruhm, 1960; *Bursaphelenchus bakeri* Ruhm, 1964
Contortylenchus diplogaster (v. Linstow, 1890)	*Anguillulina contortus typographi* (Fuchs, 1915); *Allantonema diplogaster* v. Linstow, 1890; *Aphelenchulus contortus typographi* (Fuchs, 1915); *Aphelenchulus diplogaster* (Fuchs, 1915) ; *Parasitylenchus contortus cembrae* (Fuchs, 1915); *Parasitylenchus contortus typographi* (Fuchs, 1915); *Tylenchus contortus cembrae* (Fuchs, 1915); *Tylenchus contortus typographi* Fuchs, 1915; *Tylenchus diplogaster* (v. Linstow, 1890)
Cryptaphelenchus macrogaster macrogaster (Fuchs, 1937)	*Aphelenchoides macrogaster* (Fuchs, 1937); *Aphelenchoides (Schistonchus) macrogaster* (Fuchs, 1915); *Parasitaphelenchus macrogaster* (Fuchs, 1915); *Tylenchus macrogaster* Fuchs, 1915; *Parasitaphelenchus (Cryptaphelenchus) macrogaster* (Fuchs, 1915); *Schistonchus macrogaster* (Fuchs, 1915)
Fuchsnema halleri (Fuchs, 1915)	*Diplogaster (Fuchsia) halleri* (Fuchs, 1915); *Diplogasteroides (Diplogasteroides) halleri* (Fuchs, 1915); *Rhabditolaimus halleri* Fuchs, 1915
Ektaphelenchus amitini (Fuchs, 1937)	*Aphelenchoides amitini* (Fuchs, 1937); *Parasitaphelenchus (Cryptaphelenchus) amitini* Fuchs, 1937
Ektaphelenchus typographi (Fuchs, 1930)	*Aphelenchus typographi* (Fuchs, 1930); *Parasitaphelenchus typographi* Fuchs, 1930; *Parasitaphelenchus (Ektaphelenchus) typographi* (Fuchs, 1930)
Micoletzkya buetschli acuminata (Micoletzky, 1922)	*Fuchsia buetschli acuminati* Ruhm, 1956
Neoditylenchus major (Fuchs, 1915) Meyl, 1961	*Anguillulina major* (Fuchs, 1915); *Ditylenchus major* (Fuchs, 1915); *Synchotylenchus major* (Fuchs, 1915); *Tylenchus major* Fuchs, 1915
Parasitaphelenchus sexdentati Fuchs, 1937	*Aphlenchoides uncinatus sexdentati* (Fuchs, 1937); *Parasitaphelenchus uncinatus sexdentati* Fuchs, 1937
Parasitorhabditis acuminati (Fuchs, 1915)	*Rhabditis obtusa acuminati* Fuchs, 1915; *Rhabditis (Parasitorhabditis) obtusa* f. *acuminati* (Fuchs, 1915)
Parsitorhabditis amitini (Fuchs, 1915)	*Rhabditis obtusa amitini* Fuchs, 1915; *Rhabditis (Parasitorhabditis) obtusa* f. *amitini* Fuchs, 1915
Parasitorhabditis obtusa (Fuchs, 1915)	*Parasitorhabditis typographi* (Fuchs, 1915); *Rhabditis obtusa* Fuchs, 1915; *Rhabditis obtusa typographi* Fuchs, 1915; *Rhabditis (Parasitorhabditis) obtusa* f. *typographi* Fuchs, 1915
Parasitylenchus dispar (Fuchs, 1915)	*Anguilulina dispar typographi* (Fuchs, 1915); *Aphelenchulus dispar typographis* (Fuchs, 1915); *Polymorphotylenchus typographi* (Fuchs, 1915); *Tylenchus dispar typographi* Fuchs, 1915

found on bark beetle body surface as well as in their body (e.g. *Cryptaphelenchus* and *Ektaphelenchus* species). Although considerable attention has been devoted to entomophilic nematodes associated with important pests like bark beetles, our knowledge of these nematode–beetle associations in central Europe is still limited. Furthermore, a large number of synonymous names makes the orientation in this topic more difficult. Expanding on this knowledge will be an important task for the coming years. .

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